III.—*The Origin of the Vertebrate Skeleton.*

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[Continued from vol. ix. p. 280.]

§ 3. *The Physics of the Skeleton.*

The next step after a study of growth is to observe in what directions growth usually occurs; then we may discover the forces which accumulate the energy that results in such growth. All animals of the kinds named Vertebrata have their internal bones arranged in a way which in many respects is the same for them all—a great antero-posterior extension; and this arrangement is named the skeleton. But when animals are contrasted with each other, they manifest differences in the degree of growth, and in the presence or absence of some of their bones; and these peculiarities, being persistent through an immense number of variously modified individuals, give to the skeleton a number of different plans, which admit of being defined. And out of these considerations arise the great problems affecting all bones, which will here be stated. They are:—What is the skeleton, and why has it an existence as a skeleton? and what are the plans of growth of the skeleton among vertebrate animals, and why do those plans exist?

Here, then, the skeleton first appears as an accomplished fact, without visible genesis beyond such as may be traced in each individual, where changes are observed to occur in the bones after an animal has left the egg or the uterus, which are in sequence from their first formation to completed growth.

By the skeleton, I understand in the foregoing passage the vertebrate skeleton only; and I wish, for convenience, to keep the idea of the vertebrate skeleton distinct from other important osseous machinery of vertebrates, which is better named the appendicular bones, the dermal bones, and the respiratory bones. The reason for this distinction is that the nature of their relation to the axial skeleton must first be demonstrated before it can be reasoned upon. The vertebrate skeleton, moreover, is the only one which is well developed in every vertebrate animal, the other bones being variable and giving characters to the plans of the subordinate sections. Thus the Vertebrata admit of being defined as those animals in which the elongated central nervous system is sheathed posteriorly by a sequence of osseous rings, and anteriorly by a bony box—the rings being the vertebræ protecting the spinal cord, while the box is the skull covering the brain. This definition includes all the animals classed by zoologists as Vertebrata, excepting the lancelet (*Amphioxus*), which, for reasons given in the chapter on classification, must be regarded as forming a group of equal zoological value with the Vertebrata.

The division of the nervous system and of the skeleton into a long posterior part and a wide anterior part is the essential vertebrate character. And if we are to understand what characters are essential, and why they undergo change, an attempt must be made to state clearly what they are, and why they exist. It will be sufficient, with regard to the spinal column, to know that it is a central, somewhat cylindrical mass, extending the length of the vertebral column generally, giving off at intervals pairs of nerves, and tapering towards the tail. While the brain is posteriorly continuous with the spinal cord, it is much larger, and consists of parts which are sometimes arranged one before the other, and sometimes one over the other; it usually gives off nerves to the eyes, the ears, the nose, &c.

The vertebræ have a common basis, on which the neural column rests, and which is a subcylindrical column, called the notochord. When segmented and ossified, it forms the part of each vertebra named the centrum; and this centrum gives attachment to a pair of bones which arch over the spinal cord and are separated from others by the intervertebral nerves; they may become inseparably united to the centrum or always remain distinct. The skull is made by a number of small bones which suturally unite, or simply overlap each other, so as to enclose the brain, which case usually may be separated vertically down the sutures into three more or less well-defined segments, each consisting of a bone at the base, a bone on each side for the sides of the arch, and one or two bones above vaulting it over. A necessary and separate part of the skull is comprised generally under the terms upper and lower jaws.

Now we have to inquire why these parts exist—in other words, how they come to grow. And all growth has been seen to be organic dialysis, which takes place under the influence of alternating pressure and tension and rest. How, then, does this law apply to the formation of the vertebrate skeleton, and account for the formation of bones so deeply seated and well protected, and for the formation and complexity of brains and crania? I will endeavour to explain.

All vertebrate animals are locomotive, and all fish and all immature Amphibia live in water. These animals progress backward, though we usually name the motion forward; that is, each uses its tail to obtain a leverage by which it retreats, the animal's head necessarily going where the tail sends it. It is therefore evident that the head, in piercing the water, experiences some pressure alternating with rest, while the body experiences a serpentine motion originated by the tail and passing forward. To understand clearly the effects upon the animal of this movement, it will be useful to study it experimentally. If, then, I take an ordinary long bolster, which in its cylindrical form will represent a fish, and hold firmly one extremity of it (which for convenience I suppose to be its tail), and then imitate the movement of the fish by moving the tail powerfully from side to side, it will be seen that the movement propels the feathers towards the free end of the bolster; that is, by granting the bolster a tail, I have elaborated for it a head also. Now to apply this principle to the fish. Instead of the force furnished by my hands, there are enormous muscles extending down the body; instead of the bed-ticking for an outer envelope, there is a vertebral column; and finally, instead of feathers inside of it, there is the central nervous system, which, in the young state at least, is centrally fluid. Now, if the tail is set moving as it is seen to move in a fish out of water, the powerful pressure behind will compress the light semifluid substance of the spinal cord and force it to move forward, and this movement is maintained during the life of the individual; it will also by the tension increase the length of the spinal matter relatively to the osseous sheath. The mechanical effect, then, of motion originated by the tail is an immense amount of leverage applied at every point of the curve of the body, which inevitably acts upon the contents of the spinal tube in compressing and forcing the substance forward. It also must act, as all tension and pressure have been seen to act, in stimulating the growth of the spinal cord.

Thus there is a persistent influence ever tending to elongate the spinal column. As it was seen that there is an actual forcing of the spinal cord forward, so this growth will tend in the same way. But I have already pointed out how soon the individual power to be modified in form comes to an end, although the forces capable of modifying the organism continue to act,—and that thus the energy of life is not lost, but becomes potential for a time in the parent, and can only be manifested kinetically when a bud or ovum which has in it a capacity for mobility which the parent had not, is thrown off from the organism; and then, under the name of a variety, we see manifested the potential activity of the parent which its organization had previously compelled to remain as potential activity. So that we cannot expect to find these forces producing large visible effects under our eyes in one individual. But we must expect that in a succession of individuals, each of which remains for a certain period capable of modification, the force which is potential and persistent, and in each individual is renewed, will, as the opportunities for it to take the kinetic form successively arrive, be manifested as fully as it would originally have been in one individual if the organic machinery had been capable of maintaining the nutrition necessary to elaborate growth. I shall thus be justified in reasoning about the species as though it were an individual, and to conclude that the force which has been shown, both theoretically and experimentally, to be competent to produce an elongation of the spinal cord toward the part called the head, actually does produce the effects which it ought to produce. And the way in which this is done depends upon the means to do it: first, the forcing of the nutritive fluid forward necessarily produces an enlargement of the nervous system at the anterior end; and, secondly, the growth forward of the nervous system must cause a pressure which will stimulate special growth in that region; and the parts of the brain which were originally arranged one before each other may come to be forced one over the other by growth forward of the neural tissue pressing into the brain-case.

And when a brain is examined, in it are found large cavities called ventricles, which are the receptacles of fluid, such as we might theoretically expect. And when the brains of the lower Vertebrata are compared with those of the higher Vertebrata, there will be remarked a gradual increase, as we ascend in organization, in the size of the cerebral lobes, which first push the optic lobes on each side so that the cerebrum abuts against the cerebellum, and finally overrides it. Therefore it must be anticipated that the longer the time for which a vertebrate type of animal has persisted upon the earth's surface, the higher will be its nervous organization; and hence that extinct animals which seem to be the direct representatives, so far as their bones go, of existing animals, will, so far as they approach nearer to the common vertebrate plan, have had a lower grade of vital organs. Having seen that the movement of the body would be competent, by governing the direction of growth and the distribution of nutriment, to generate the brain from a pre-existing spinal cord, it is probable that the nerves are in the same way affluents to and sustainers of the spinal column, and that their presence preserves its division into segments.

Having advanced this hypothesis of the vertebrate plan of the central neural system, we will endeavour to see how the nerve-matter becomes coated with the investing skeleton. And to do this, it will be requisite to consider the entire body as a machine capable of manifesting the forces of pressure and tension, and to examine how the part of the body under consideration can be affected by these forces.

It is due to Mr. Herbert Spencer to state that he has endeavoured to grapple with this question; but, although he appreciated fully the simple mechanical conditions of the problem, he seems to me to have failed to solve it. His argument is that when pressure is manifested on alternate sides of a rod, there will be a neutral axis within it which only experiences small compressions, and external to that an investing region, where pressure and tension alternate. He then tries to apply that principle to a fish. The principle would be perfectly applicable to a long bone, and would account for its being hollow or less dense internally; but it is not applicable to a fish, because there is nothing to correspond to the hollowness of a bone in the middle line of the animal; and, on the contrary, the region which should be the unossified neutral axis is the ossified neural skeleton—a condition exactly the reverse of what it should be were Mr. Spencer's hypothesis true. Mr. Spencer's error consists in not recognizing that the muscles of the body are, in regard to the production of the neural skeleton, precisely what the weight is which bends a revolving flexible rod—the power which produces a neutral axis, and which also produces the pressure and tension in which we have seen that ossifications arise*.

In seeking to explain this formation of an osseous skeleton, instead of taking an abstract, impossible archetype to reason from, my argument may be clearer if we examine the conditions of the problem as presented in some animal. Having the choice of animals, among which a Chelonian would be the least suitable, the most difficult skeleton to understand, I select a whiting. The fish manifests locomotive energy; and to find the source of this mechanical power, I skin her. The skin requires to be dissected off, on account of its close union with the constituent fibres of the muscles; and in some parts of the body there are attached to it special skin-muscles in addition. The skin removed, there is seen an enormous development of muscles, which are arranged in a very marked way. Fibres extend from the skin obliquely inward toward the skeleton; and these fibres are grouped into obliquely placed muscles, which are arranged along the animal parallel to each other, so as to make large strips of similar muscles, which reach from tail to head. In the tail of the whiting there are four of these strips on each side; and the constituent muscles are so arranged that the obliquity of the

* Principles of Biology, vol. ii. p. 196.

four series makes a W-like outline when traced externally from the dorsal to the ventral surface, the upper part of the W being towards the animal's head. Here, then, is an immense muscular power, so arranged as to act in many directions.

Removing the whole of the muscles, we expose the vertebrate skeleton beneath them, and find that each transverse muscular segment corresponds with a transverse osseous segment; and that the direction of the muscles of the two middle strips of the W coincides with the direction of the dorsal and abdominal processes of the vertebræ, and with the nerves. These middle muscular strips are large compared with the superior and inferior strips; and in transverse section each often shows, by the method of overlapping, an approach to a concentric arrangement of the constituent muscles in the region of the tail. The forces represented by these muscles are, I believe, precisely such in their distribution and combination as theoretically might have been anticipated. But, before considering the effects of their action, it is to be remarked that the discovery of a notochord among the Tunicata lends strong probability to the supposition that the notochord, which extends beneath the neural chord, is not a product, but one of the original foundations, of the vertebrate plan. But, granting a notochord, it is impossible, without a stretch of imagination, under which the reason gives way, to assume the existence of a mass of muscle like that which makes the great bulk of a fish, and then try to account for its segmented condition, as Mr. Herbert Spencer does, by lateral breaking strains. In nature, so far as I am aware, no such phenomenon exists. And it seems to me as gratuitous to assume the existence of the muscles, in order to have them subsequently segmented by these imaginary lateral strains, produced without any force to produce them, as it is to suppose that the foundation of the vertebral column is laid by breaking strains segmenting the notochord. Before such views can claim to be considered in science, their author is bound to show that an animal is acted upon by lateral forces external to itself, and that an effect of such strains would be to cause the muscular tissues to snap into little short muscles, and that such strains continued would eventually pass through the whole of the animal except its skin and viscera! In the chapter on growth, we have seen that the consequences of strains would be, not a weakening, but a strengthening of the tissues.

In the axial part of a fish, a serpent, or indeed in any animal, the successive segments, both of bone and muscle, are exceedingly similar to each other. Almost at all parts of the trunk two adjacent vertebræ can only be distinguished from each other by close comparison, if they are in the same division of the body. And there being this sequence, the form of parts only changing with the changed function of different regions of the body, it will be legitimate reasoning, if we can discover a law capable of accounting for a primitive initial segment, to conclude that the continuous operation of that law would eventually segment the entire animal, *if an animal capable of being encased in a segmented covering already existed.*

According to the laws of growth, we find that differentiation of parts is due to the kinetic energy of the individual or to the potential energy of its organization—and that no organic energy is lost, but becomes accumulated in the individual long after the mobility of the parts ceases, and then is transmitted with and added to the common stock of energy to be inherited. If this inherited energy is such that it is capable of being manifested within the mobile period of life, then it will stamp its characteristic marks upon the organism. But if it is too general to be manifested during that period, it takes a potential form, and may even remain latent for several generations and accumulate, and then, instead of being developed kinetically in the individual, it at an early period is merged in the common stock, and appears kinetically in the organization, and potentially in the individual, as a new part.

Thus in Ophidians, which exert continually an intense muscular force upon every joint of the vertebral column, we find that the kinetic energy is manifested in giving to the bones great density, sharpness of definition, and perfect ossification, but never in the partial formation of a growth like an epiphysis, between vertebræ. Yet, if the views which I urge are true views, there should be some result, in increased ossification, of all this muscular power; and the result is found in the numerical increase of the vertebræ, so that in Ophidians they sometimes number 400 or 500. But this increase is potential, and takes place at so early a period that the newly added segment (vertebræ, muscles, nerves, &c.) is developed equally with the others. If the increase takes place in the thoracic region, it necessarily elongates the viscera; if the tail is lengthened, by comparison the body appears to be shortened.

If we take another type, that of the Anurous Amphibia, which do not display muscular power by wrigglings which press and pull the vertebræ, as among serpents, but progress by leaping, and keep the body removed from the ground, except at the caudal style, the power, both kinetic and potential, acts chiefly on the limbs—kinetically in the elongation and hollowness of the limb-bones, the ilia, &c., potentially (perhaps) in the formation of investing epiphyses at their ends—but in scarcely an appreciable way upon the vertebræ in either form, since they remain both very few in number and short.

It cannot be necessary to multiply these illustrations; for the same law may be traced in every osseous structure. Where an animal uses any part of the body, the part grows long, either kinetically by lengthening the individual parts, or potentially by increasing their number.

If, now, we generalize these facts in relation to the vertebral column, the result is, that since the potential epiphyses multiply indefinitely and elongate the body, so there must have been a period when the body was short and when the segments were very few—and that the elongation of the body proceeds gradually, and, except in the caudal region, is likely to be arrested by the development of limbs.

It were simplest to assume, if there had been grounds for doing so, a single vertebra as the basis from which the body was formed; but the existence of a notochord among tunicaries, and the vast gap between *Amphioxus* and ordinary vertebrates, does not warrant such an assumption; nor does it indeed enter practically into my theory of a vertebrate. However, if we assume an animal with the viscera of a fish, with a notochord, and with terminal muscles capable of moving the tail, then the consequence of that arrangement would be the formation of a terminal segment, not by breaking a piece off the notochord, but by the muscular action increasing the density of the terminal portion, and this organic dialysis eventually giving it a structure by which it is chemically separated from the other parts. The direction of the mechanical strain becomes the direction of greatest density, and determines the directions in which the osseous matter is deposited and the shapes which it assumes.

Then, just as the inherited energy of many individuals at last became a force sufficient to differentiate the first osseous caudal segment, so the continuous operation of the same muscles goes on accumulating energy for which there can be no outlet in the adult organization, and the energy takes the potential form. It has, in fact, become so powerful that, instead of displaying itself only in maturity, it begins to act upon the immature animal at as early a time as the other and ordinary laws of its growth, and in this way gives expression to itself, differentiating a new segment similar to the preexisting segment—a potential epiphysis, which, growing continuously with the original segment, can afterwards scarcely be distinguished from it. Thus the tail comes to have two segments; and so the process must go on, the vertebræ increasing in number and extending further towards the head, till the basis of a vertebral column is elaborated. So far as I am aware, this hypothesis is in accord with the sum of the facts, and gives an explanation of their relation to each other. And not only does it account for the original existence of a vertebral column, but for its subsequent modifications, and for the repetition of the successive similar soft parts (muscles and nerves) which are correlated with the bones.

But so far we only account for the centrum of a vertebra. In our usual conception of it, especially as seen in the fish's tail, it includes an arch on the dorsal part, called the neural arch, which covers the neural column, and a similar arch on the ventral side, called the hæmal arch, which covers a blood-vessel. In dissecting a fish, the muscles in the tail of the dorsal and hæmal sides of the animal are seen to be as like each other as are the neural and hæmal arches; so that it will be in accord with the mechanical basis on which this investigation started to conclude that in both cases a like force has produced a like result.

But how? If we grant the differentiation of an initial caudal segment of the notochord by muscular power, then as those lateral muscles of the tail, acting obliquely, enlarge, they would, with increasing force, become competent to set up a separate ossification upon the notochord at each of the margins of their overgrowth. And these points, it is to be remarked, coincide with the points of origin from the centrum of the lateral parts of the two arches. When once these kinetic epiphyses are brought into existence, the lateral muscular attachment would ensure their growth, and the dorsal and ventral muscles would as surely draw them towards each other above and below. Thus the fundamental plan of the tail of a fish in its soft parts supplies the machinery necessary to elaborate the hard parts; and from their less bulk and the greater relative power brought to bear upon them, it would seem not improbable that the neural and hæmal arches should be ossified at an earlier period in the history of the organization than the centrum. And this muscular power would be competent, if the arches long remained separate from the centrum, to draw them towards each other, so that the dorsal part of every neural arch would abut against the dorsal part of the arch next behind it. Thus there will come to be formed interlocking facets between the arches, of which the anterior will look upward while the posterior will look downward: in most animals the neural arches actually have such facets, which are known as anterior and posterior zygapophyses.

In the median lateral line between the great lateral muscles slight transverse processes are sometimes developed; and these may be upon the centrum, or upon the neural arch, or upon the hæmal arch, according to the arrangement of the muscles. But the point is one of detail, and not a fundamental part of the vertebrate common plan. As the caudal vertebræ progress forward towards the head, they encounter the viscera on the hæmal side; and then the hæmal arch widens and embraces the viscera, so that the parts called hæmapophyses, which in the tail are directed downward, come in the thorax to be lifted up the side of the centrum and directed outward, sometimes attached to the median lateral osseous process, and often connate with it. When the viscera extend to a great length down the body, the lateral transverse processes are not developed as distinct processes; when the viscera have a short extension and the tail is long, they are considerably developed, and then pass forward as epiphyses upon the visceral region, being developed at the point of junction of the hæmapophysis with the part of the centrum which supports it. In this form the hæmal arch is called a rib. And as the arch widens, new elements come to be introduced into the circle which it constitutes—formed toward the ventral surface by the increased expansion given to the ventral strips of muscles, which often become blended with the lower lateral strips.

In this way I conceive the vertebrate common plan to have been elaborated, so far as its osteological structures are concerned, by the mechanical machinery with which it is inevitably accompanied. And if so, it will be evident that all subsequent variations it may assume in form will be due to a different distribution of the muscular machinery resulting from kinetic growth, while the different proportions of the different regions of the column will be due to potential growth.

In first conceiving of a vertebrate I introduced two ideas—the tail and its product, the head. In obtaining a similar generalized idea of the head to that just given of the body, it may be as well to remark:—that the extension forward of the vertebræ will have maintained the spinal cord of approximately uniform size up to the point where, like the constricted neck of a bottle, it abuts against the enlarged terminal part; and that the transition in the dorsal region from neural matter covered by a vertebra to the brain covered by the skull is not dissimilar in kind to the transition seen on the hæmal surface, where the tail suddenly expands and covers the viscera, only with this difference—that while the brain experiences but very slight fluctuations in size, the viscera are constantly undergoing change. Both hæmal and neural parts terminate in the head, but under these different conditions—that while the neural arch is being modified for the first time, the hæmal arch undergoes its second transformation, which may be altered to some extent by the relation of the two arches to each other; so that, on *à priori* grounds, the hæmal arch in the skull may be expected to be more complex than the neural arch, and also to more readily assimilate to the hæmal arches of the body.

Now, if the brain-substance is supposed to have accumulated at the anterior end of the body as a consequence of the motion and mode of growth of the animal, and quite irrespective of the vertebræ, its covering from the very first experienced some different conditions of ossification from those of the vertebral neural arch—supposing, of course, an anterior enlargement of the nervous system to have taken place prior to the entire segmentation of the notochord. Such a view, however, is not supported by the evidence from *Amphioxus*, since the notochord is segmented and no brain developed. And the difficulty of a theory of the skull hinges upon the relative probability of the skull originating prior or subsequently to segmentation of the notochord—because in the one case it will be but an extension onward of the vertebral plan, and in the other case it may have originated apart from the vertebral basis. If the *Amphioxus* is a distinct type animal from the Vertebrata, we shall not be warranted in reasoning from it to a vertebrate. But, whatever the initial circumstances were which governed the formation of a brain-case, we shall not be justified, except with good evidence, in assuming any other cause to account for it than potential repetition, which under altered conditions has been found competent to produce very different osseous structures in different parts of the vertebral column, especially as the brain offers a surface to be covered different from the spinal cord, and conditions of stability different from the visceral region. It has been seen, with the diverging vertebral processes, that, under the new conditions, osseous elements come into existence which were not found in the caudal region: similarly it will not be surprising if some new structures are developed in the head by the special influences working in that part of the body.

Suggestive evidence of original unity of origin, direct or indirect, for the whole skeleton, is supplied by the skull being segmented, as it is shown to be by well-made researches; for if it had originated independently, no trace of segments could be anticipated, but an arrangement of bones with which the spinal column would have at first nothing in common, though eventually its potential energy would influence their arrangement, and gradually bring the structure of the brain-case into harmony with the vertebral plan. Thus there are three possible ways of formation for a skull:—1st, potential repetition of the vertebrate plan; 2ndly, independent ossification; and, 3rdly, independent ossification modified by potential repetition. The facts of the case are such that it is quite possible to select examples which would sustain each of these views. Thus among the shark tribe, the bony cerebral envelope is made up of homogeneous osseous particles which show no indication whatever of segmentation. And, in the absence of evidence of division of the head into separate bones, it would be an unwarrantable use of the imagination to suppose that the divisions had once existed and have become obliterated. This would seem to be a type of those examples of the skull which have originated independently of the vertebral column and before it extended the whole length of the animal. The serpent might be taken as a type in which the skull might have originated as a natural consecutive part of the vertebral system; while for the third type we might instance fishes like the sturgeon or animals like the Chelonians, where the brain is first sheathed in homogeneous cartilage which may have been formed independently of the vertebral system, then this is covered with osseous plates, which reproduce with some modifications the vertebral elements.

Thus there must always be a conflict between potential energy, in organization, leading to uniformity and simplicity, and kinetic energy, leading to variety; and the longer any type endures in time, the more closely its cerebral region will approximate to the vertebral structure, so far as the grouping of the bones is concerned; thus in the human subject the structure of the brain-case is more simple and the segments are better marked than is the case with fishes; so that a theory of the skull will depend upon the organization of the animal, which determines the relative influence of kinetic and potential ossification.

The human brain-case, being almost entirely a potential ossification, is one of the simplest. It consists of some (three) bones at the base, in the median line, called in sequence basioccipital, basisphenoid, and presphenoid, the basisphenoid and presphenoid in the adult being united together as one bone. The basioccipital immediately follows the centrum of a vertebra; and these bones are to the skull what the centrums would be to three segments of the vertebral column. On each side of this row of skull-bones are placed three other bones (a side bone to each base-bone), which rise up to embrace the sides of the brain. They are called (in sequence from behind forward) exoccipital, alisphenoid, and orbitosphenoid, and have the same sort of relation to the base-bones that the lateral elements of the upper arch of a series of three vertebræ have to the three centrums out of which they rise. In the vertebræ the upper bones, called neurapophyses, enclose the neural substance, meeting above it. In the skull they do not meet above; but just as with the lateral elements of the inferior vertebral arch, in the transition from the true caudal region to the preanal or visceral region osseous elements come to be introduced between them in some animals, which did not exist in the tail, so in the transition from the upper arches of the vertebræ to the upper arches of the skull, enlarged to cover the brain, a sequence of bones is introduced, to roof over the cavity, to which there is nothing corresponding in the vertebral region. These bones, counting from behind forward, are named supraoccipital, parietal, and frontal. And all the bones enumerated differ from those of vertebræ in touching each other throughout their lateral margins by sutures or overlap—a condition which in the vertebral column is only met with exceptionally, as in the cervical region of the rays, pipe-fish, &c., and a part of the vertebral column called the sacrum, in many land-animals. And these bones touching each other throughout their extent, enlarge the cranial cavity much in the same way as a sea-urchin enlarges its covering shell. In the human skull there is something more, however; there are bones which have existence in relation to the senses: such are some bones which come in between the first and second segments of the skull, and are connected in a more or less evident way with the ear; they have been named collectively the otic bones. Then, between the second and third segments, though external to them, is usually one bone or more, developed seemingly in relation to the eye: the lachrymal (and, perhaps, the malar) is such a bone. And in front of the brain there are bones which have relation to the nasal functions, and are named generally the ethmoid bones. In possessing these sets of bones the bony investing girdles of the brain differ in plan from the investing girdles of the spinal column.

If, now, we ask why there should be three segments in this bony box for the brain, and why not an indefinite number of segments as in the vertebral column, and why the structure of the skull should become simpler the higher we ascend in nervous organization, so that the three segments become more and more well defined, the answer is, that the division between the segments is maintained by senses which are not repetitions of each other, that the brain has a terminal sense anteriorly, and that by the bones touching each other on every margin, along all of which they can grow, there is in the skull an exercised facility for kinetic growth, which renders it impossible that potential growth should be manifested. If, for instance, a potential epiphysis of the frontal segment of the skull were to be formed, it could only be developed between that segment and the parietal segment; and it could only reproduce, to mark its division, a new pair of eyes behind the old pair. And it is impossible to conceive of such a change taking place except as the only way in which the energy of the animal could be manifested. While, therefore, the bones of each segment remain separate from each other, and permit growth within, it is impossible that any cerebral increase, supposing for a moment it were competent for such an end under any circumstances, could result in the formation of a new segment. Then (no matter how the mammalian skull originated), being segmented by the sense-capsules, it must ever have been subjected with greater and increasing influence to the potential power of the vertebral column, which will be manifested in bringing the plan of the segments of the skull more and more into harmony with the plan of the vertebræ, and so will obliterate any differences due to origin or number that there may have been, in an earlier condition, between the structures of the different segments.

Neglecting for the present the jaws of the potential skull and the whole question of the nature of the inferior arches to the segments, I would draw attention to the question whether the potential character is always an induced one.

In most sharks there is no differentiation whatever of the brain-case into constituent bones. In a specimen of the angel shark in the Museum of the Royal College of Surgeons, there appears on the base of the skull to be a faint indication of a transverse division. And it might be presumed that the segments would originate first, and then that each segment would put on the divided condition; but I doubt whether the tendency to potential increase is the same in the neural arch and centrum; for in many sharks the neural arch appears to be double, to have been formed originally at each end of the centrum, though often one of these arches has more the aspect of a supplementary arch introduced between two centrums; moreover the fact that in palæozoic fossil fishes the centrum is rarely ossified would lead us to anticipate that in the skull the base-bones would be the last formed and least well defined; so that in conceiving of a skull induced potentially upon the basis of a shark's skull, it would be quite consistent with the vertebrate plan to have a greater number of superior arches than of median base-bones.

But in those ordinary osseous fishes in which the several bones can be separated from each other, we find the skull in no transitional state, but already with the elements well defined, except at the base of the skull, where the kinetic ossification persists as a long median bone called the parasphenoid or basitemporal. And in the upper part of the skull, besides the three ordinary arches such as have been described, there come to be introduced three additional, imperfect arches, analogous to the intervertebral neural arches of sharks, and which I interpret as potential representatives of those structures. The first pair, in front of the frontal bones, are named the prefrontal bones, one on each side; the second pair are between the frontal bones and parietal, and are named postfrontal; the third set are between the occipital and parietal, and are named the interparietal bones: these latter only persist in the skulls of the higher Vertebrata.

It is to be remarked that in fishes the cranial bones overlap each other in the squamous way in which an ordinary zygapophysis laps upon its fellow.

And it appears to me probable that Prof. Owen truly appreciated the homology of the bones which roof in the skull when he compared them to the small ossification which often crowns the spinous part of the vertebral neural arch, which is by him named the neural spine, since without that ossification it would be more difficult to see why the lateral bones should not curve upward and roof in the cranium.

It is also worth considering whether in osseous fishes the potential growth may not have a direction, so to speak, given it by the influence of cerebral form, because it is observed, in skulls of equal size, that in *Lophius*, which has the cerebellum very short and small, the occipital region of the skull only measures 2 inches in length, while in the tunny, which has the cerebellum large, the occipital part of the skull measures 4½ inches in length; so that, since some fishes (like the eels) have olfactory lobes to the brain almost as large as the cerebrum, it may not be impossible that such a condition in fishes may have had a tendency to promote differentiation like that seen in the separation of nasal bones from the prefrontal in some Chelonians.

Now, just as in the more osseous fishes the parts of the divided neural arch become blended, and the centrum becomes more solid, so in the higher Vertebrata the prefrontal and postfrontal bones have become lost under the uniformity induced by potential growth—if ancestors of such animals are considered ever to have had such bones.

This being, as I suppose, the mode of origin and plan of growth of the neural arches of the skull, I turn to explain the inferior arches.

In sharks the head is singularly instructive in the relation of the jaws to the skull; for there they are seen to be free structures which are merely appended to the brain-case. This condition, permanent in the shark, is embryonic in what are called higher Vertebrata.

The jaws are the entrance to the digestive canal; and therefore we must anticipate that they will be surrounded with bones which are the representatives of those which encompass the digestive organs in the region of the vertebral column, viz. of ribs. Prof. Rathke, describing the embryonic development of the jaws in serpents, records that "that part of the investing mass of the notochord in which the basisphenoid is developed in many animals sends out a 'ray' or band downwards on each side, which presents a remarkable similarity to a rib, not only in its mode of origin, but in its original position and form." "But very early there grows out from near the upper end of the ray a long thin process, which passes off at an obtuse angle to it, and applies itself to the inferior wall of the future brain-case." Now this condition is that of an ordinary rib of a fish. There is a long rib, as in mammals; but near its junction with the vertebra it gives off by articulation a long thin epipleural element, homologous with that of Crocodiles, *Hatteria*, Birds, &c.; so that I see no reason to doubt that the jaws are developed primarily as one rib, the epipleural elements of the two sides being directed forward and meeting in the middle line, so as to form the palate, and the ordinary pleural elements being directed downward so as to meet and enclose the digestive tube below. The ribs of fishes are simple; but in reptiles and birds and mammals they become segmented; and there appears to be no limit to the number of parts which may be included, while the degree of ossification is various. In some animals there are five parts.

In the serpent the epipleural element becomes segmented into the pterygoid, palatine, and maxillary bones; while the rib itself is divided into the quadrate bone proximally, then the articular bone, and then the elements of the lower jaw, which surround the cartilage and may number as many as five. The cranial representative of the rib always articulates with the squamosal bone.

It must at once occur to any one to ask, if the cranium consists of three segments, and only the middle one developes a rib, what has become of the ribs to the other segments? And it was the difficulty that there is in meeting this question in the higher Vertebrata, which led me (in a former paper*) to regard the occipital and frontal segments of the skull as standing in the same relation to the parietal segment as the epiphyses of a vertebra stand to its centrum. But remembering that, no matter what the potential power may be, it can only give great development to a structure when coincident with functional growth, we should no more be justified in anticipating ribs to all the cranial segments than to all the vertebral segments; and with many animals parts of the vertebral column will be devoid of ribs. Yet as the upper arches of the skull retain characters which long previously became lost to the upper arches of the vertebral column, so we might with more reason expect the lower arches to be present in the skull than in cervical or lumbar vertebræ. Accordingly, if we examine a skull, and remove all those bones which we have regarded as modified from a functionally developed rib (which we name the jaws), there will be found in front of their point of attachment, and under the frontal segment, two bones, named the vomeres; sometimes they become anchylosed into one median bone. And anterior to these bones, and bent up over them frequently, are the ethmoid bones, which similarly may become anchylosed. Thus we again have the representative of a rib with its epipleuron. By segmentation the ethmoid developes the nasal bones; and it is probable that by segmentation the vomer forms the premaxillary. Thus the anterior rib conforms in plan to the posterior rib, and, like it, embraces an organ which, in the lower animals, is only that of smell, but which, by potential growth comes, in the higher vertebrates, to be the respiratory region. So that, just as there are distinct tubes for breathing and for swallowing in the land Vertebrata, so distinct tubes are made for those offices in the skull by the prolongation forward of the dorsal respiratory tube till it is embraced by the first pair of cranial ribs, while the digestive tube, not prolonged so far forward, is embraced by the second pair.

It is not so easy to find the third pair; and only on turning to the fish is the homology evident. At each side of the back of the skull is a bone attached to the periotic bones, named the hyomandibular; and to this bone is attached in front the circle of hyoid bones; and attached to it behind are the opercular bones; so that there is again a forked rib variously segmented for the third arch.

* "Outline of a Theory of the Skull &c.," Annals, 1866, xviii. p. 345.

With the termination of branchial respiration (and the branchial arches appear to represent the epipleural elements of cervical ribs) the function of the pleural element of the first cerebral arch appears to cease, and the bones of the operculum are no longer developed; and in the same way, when the respiratory function becomes changed, so that the animal breathes by lungs, the branchial bones are merged in the hyoid; the hyoid loses its heavy osseous character, and has a less firm attachment to the hyomandibular. This bone then gives attachment to the quadrate, and becomes the main support for the mandible; so that it appears to be the bone which among the higher Vertebrata is named the squamosal. In the fish there are bones in front of the quadrate bone which are called metapterygoid and symplectic. I have doubted whether these bones may not have originally stood in the same relation to the second visceral arch which the hyomandibular held for the first, since they persist, the metapterygoid becoming the quadrato-jugal, and the symplectic becoming the supraquadrate; and they both appear ultimately to be absorbed into the squamosal. If this view were taken, it would in no way be inconsistent with fact, and would only show that the lower jaw had been carried a stage backward, while it would explain the existence of two otherwise obscure bones, and justify their disappearance under the influence of potential growth in those animals in which they are wanting, since in the Amphibia is seen a similar lateral joining-up and absorption of the branchial arches into the hyoid.

Already it has been remarked that the lower jaw always articulates with the squamosal bone, the squamosal bone being, as we have just seen, apparently the proximal element of a visceral arch. Sometimes the squamosal bone itself is free, as in serpents; but usually it is firmly fixed in the skull. Sometimes, also, the quadrate bone is firmly wedged in the skull, as in Crocodiles, Chelonians, *Hatteria*, and most of the extinct Monocondylia; but there is no evidence whatever of any other part of the lower jaw (as the os articulare) being united with the skull. And in all those animals in which the quadrate bone is joined with the skull, the lower jaw remains composite. In the highest Monocondylia (birds) the quadrate bone remains distinct, while the squamosal bone has entered into the skull in the same way as in mammals, and furnishes a concave articulation for the quadrate bone exactly like that which in mammals is given to the lower jaw. Now, in so far as the lower jaw occupies the position of a rib, the influence of potential growth upon it would be to make it ever more and more like a rib in simplicity of structure: hence I presume that when, in the mammal, one continuous ossification joined up all the splint elements of the lower jaw, the os articulare and quadrate bone, as natural elements of the same rib, could be no exception, and that there is nothing more remarkable in this union than in any of the other transitions to simplicity and uniformity and order which are produced by potential growth.

And it may not be uninteresting to remark how much the vertical part of the lower jaw in any herbivore reproduces of the form of the quadrate bone in such an animal as a bird, and how the inflection of the lower jaw in marsupials and rodents reproduces such an inflexion as characterizes the os articulare in birds and many reptiles. These growths in the mammal may, I conceive, be potential repetitions. In the mammal the pterygoid is moderately developed and is directed downward posteriorly, and not backward as in birds and lizards; so that it does not actually meet the representative of the quadrate bone; but the union is kept up by the pterygoideus muscle, attached from the outer inferior side of the pterygoid to the inner side of the quadrate portion of the lower jaw.

I am aware that Prof. Huxley has supposed that, contrary to all analogy, the quadrate bone and os articulare enter the mammalian cranium and become the malleus and incus. After reading all that has been said for that doctrine, I can see no evidence in its favour sufficiently strong to dissuade me from stating my own view. If it has been important to construct those bones out of pre-existing cranial elements, I would suggest that Prof. Huxley might have taken the quadrato-jugal and symplectic, which were available and would have answered equally well. But I do not think any exigency of theory can justify the creation of a new joint in the body by imagining a convex articulation beneath the articular bone, when there is nothing in the vertebrate province to suggest that such an articulation might exist.

Such, divested of details, is the conception of the common plan of the axial skeleton which, by the operation of the laws of organic energy, may, I believe, call all skeletons into existence, extending them over the viscera like a pillow-case over a pillow, till the animal is gradually but inevitably sheathed in rings of bones. And thus it will be remarked that the pre-existing soft animal would have no necessary correlation of soft vital parts with its osseous sheath.

I touch with reluctance, because of its difficulties, on another part of the skeleton, which seems as though only appended to the vertebral column, already discussed by Prof. Owen, in his treatise on limbs, and by others. Each limb consists of a sequence of bones, of which the number of parts in each segment in most animals increases from above downward, and is usually the same, part for part, in the fore limb and in the hind limb. Thus in the first segment there is one bone, the humerus or femur; in the second segment two bones, the ulna and radius or the tibia and fibula; in the third segment three bones, in the proximal row of the carpals or tarsals; in the fourth segment four bones, in the distal row of the carpus or tarsus; and in the fifth segment the five digits. Variations occur in great number, but chiefly by suppression of parts; and so true is the correspondence in general, that Professor Humphrey offered an interpretation of the structure by supposing that there were originally in each limb five rays, which in the humerus are blended into one, while in the phalanges they remain more frequently distinct.

It will be necessary to ask, what are these limbs, and in obedience to what mechanical law are they where found, and why do the fore and hind limbs correspond in their parts?

But, besides the limbs, the skeleton possesses the arches with which they articulate:—for the hind limb a pelvis, made up of an ilium, ischium, and a pubis; and for the fore limb a scapular arch consisting of a scapula and coracoid, and sometimes having associated with it a clavicle and interclavicle.

If we turn to comparative anatomy for an explanation of the phenomena, in sharks and rays the pectoral and pelvic regions will be found to be well developed, and long limbs are attached to them which are already well segmented and limited at the sides to fore limbs and hind limbs. In osseous fishes, however, the fins represent, as a rule, more than two pairs, and are often strongly developed down the back. So the first difficulty is, why should there be but two pairs of limbs? To that question, perhaps, an examination of a skeleton will furnish an answer; for the two arches will be seen to be at the two ends of the primitive soft animal enclosed by the skeleton, and at the two chief points of flexure of the skeleton—one where the neck bends with the body, the other where the tail bends with the body; and in those animals in which there is little or no special flexure in one part more than another, limbs are wanting, the potential tendency to the development of limbs nevertheless notwithstanding. Now if we can discover why they are wanting, we obtain a clue to their law of development.

In serpents the power expended in motion is distributed equally along the whole body, and there is scarcely greater pressure in one part than in another; so that its influence upon growth is only seen in the great length of the ribs. Now, if the body were stiffer in the middle, and flexible chiefly in the neck and tail, then, instead of intermittent pressure being distributed uniformly, it would be manifested chiefly at the two extremities of the stiffer part, which, touching the ground, would be lifted by the movements of the head and tail. If, then, a large part of the pressure and tension which, distributed over the body, elongate the ribs of Ophidians, were accumulated in this or some such way (by movement of the body) at these points, whatever osseous structures pre-existed there would grow; and potential growth would tend to make the parts at the anterior end of the body correspond with those at the posterior end. What parts, then, would there be existing in such places? Clearly some element of the abdominal rib—elements, it may be presumed, which become the coracoid bones and the ischia. As the ribs become segmented into a number of parts in different animals, it is not easy to guess how many were developed; but as the facts of the case only require two (coracoid and scapula, and ilium and ischium), these may be presumed to be the second and third segments of the rib. Now the consequence of setting up a special tendency to grow in these elements can in no way interfere with the growth of the original rib, which, being joined to these hæmal elements by overlap and by muscles, would, I suppose, slide over the outside of these new growths, which would extend inside of it. And I should regard the epipleuron as eventually forming the clavicle and the pubis, while the suprascapular is an effort of potential growth to reproduce the original rib from which the arch-elements have become detached.

But how account for the limbs? Did they spring into existence ready formed, or grow gradually? and, in either case, how? I cannot but be impressed with the forked character of the limb, dividing in its second segment, as reproducing the forked character of the visceral arches of the cranium and of the vertebræ; and therefore I believe that, in the absence of any other evidence of a distal osseous fork, we can only look for the proximal element of a limb in the proximal element of a rib. And so I conceive that the increased muscular power of the pectoral or pelvic girdle might detach the proximal part of the rib from its attachment with the vertebra and draw it on to the already expanded hæmal elements—and that potential growth, such as reproduces the lizard's tail and the salamander's legs, would cause its distal segments to be developed anew at the distal end, although the proper distal segments now gave attachment to the proximal end. With the bone would necessarily follow the muscles; and potentially added segments would comprise both hard and soft parts. In the absence of evidence, I can only throw out this idea as completing a conception of the skeleton as a whole. It explains the origin of limbs simply as a modification of pre-existing structures, without calling any new part into existence; it explains the harmonious segmentation of fore and hind limbs, and the increase in number of bones in the successive distal segments (as well as the primitive separation of the arches from the vertebræ), which are the fundamental points of structure in a limb. And no idea of epigenesis from the arches, as suggested by Professor Owen, could justify either one condition or the other. The only other obvious origin for the limbs is by potential growth repeating the structure of the jaws with their segments upon each of the arches, first on the pectoral and afterwards on the pelvic arch, which is simple and so far a preferable view. And if the limbs were regarded as potential jaws, the fact that there are thus two modified appendages to the body may explain why the three segments of the brain-case have only one functionally developed hæmal arch, the other two, by potential growth, being removed to the pectoral and pelvic arches.

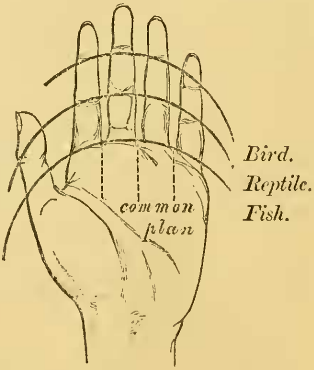
This conception of the skeleton as originating in a single ossification, and attaining all its complexity by growth in a definite direction, which is sustained by laws coextensive with the universe, and modified in the limbs by the circumstances of existence, has a unity of plan, and gives a reason for every variation which it displays. And if we believe that animals have been changed in form and stature by the continuous operation of those laws of energy which, by changing the minutiæ of every thing that cognizance extends to, preserves for them uniformity, order, and progress, then such small variations from this common plan as give the distinctive marks to each group of animals are themselves but an evidence of the larger range of those laws which give the animal its unity and one harmonious government with all things. Because this unity is incontestable, I believe in this change as a condition of its stability; but whether it is named creation or whether it is named evolution, no name can extinguish the unbounded harmony of the relations which it exhibits, or the unvarying order in the changes to which names are but paths, or can part a knowledge of the universe in its government from an unutterable and reverent confidence. For to me it indicates, beyond laws and their consequences, what, judged by human standards, is Intelligence, of which laws in their working are manifestations. If, then, an attempt is made to explain the plans of animal life, it is in faith, born of science, that they are products of divine law, and in a conviction of duty to seek out its working in all ways.

The scheme of the skeleton now sketched is what may be named a potential skeleton; and whatever value it has is in the insight it gives into the relations to each other of the parts of skeletons and the importance of resemblances between similar parts in different skeletons as evidence of genetic relation. All the types of vertebrate animals are based upon this general plan, and each differs from the other in some comparatively slight details of potential growth; and there is nothing peculiar in the genera referable to each of these minor types except a varying growth, or suppression of growth, or combinations of growths in the different bones of the body: such modifications are the kinetic skeleton. If we find similitudes between bones when they are compared together, the comparison becomes meaningless and unprofitable unless we believe the similitudes to be consequences of laws which can be traced in their effects. The idea of affinity expresses faith in such laws by teaching that the structural resemblances between animals are a consequence and evidence of an original community of plan now only seen in fragments. And an original common plan for vertebrates, a potential skeleton, implies that the physical laws of nature producing growth have upon their simpler product acted in differing ways, so that the energy of the type became manifest in the divergence of special different parts which make the plans of the several vertebrate classes.

Hence the practical question, affecting all comparative study, after the mind has cancelled whatever osteological structures are variable in the type (and therefore demonstrably kinetic), is to discover in what direction each order has diverged from the common plan, and in what way this diversity obscures or renders clear its affinities with the other orders. To put a special case:—in what direction relatively to the vertebrate common plan is the osteology of a tortoise developed? and how far from this osteology can we infer a community of divergence between the tortoise and all other or any other known animals? Those points of divergence in the potential skeleton would be the osteological affinities of an animal, and, determined for a number of known types, would enable us to predicate within approximate limits the characters of many extinct orders of which the existence is at present hardly suspected.

To examine such a problem, it is necessary to be familiar with the facts which are factors in it; and so to these we must next turn.

The correspondence of parts is frequently close between animals which would not be placed by classifiers in the same natural group; so that, as animals can only have diverged in many different directions, or in directions which are approximately parallel, it is impossible not to believe that the correspondence is the evidence of some kind of parallel relation between the groups, which may, of course, be a parallel function kinetically modifying different common plans, or parallel plans kinetically modified by different functions. Each vertebrate class consists of orders, but if these are arranged in sequence of classificational semblance, their bones do not graduate from one group into another: the lowest mammal does not graduate into the highest bird, nor is there a sequence from the bird down to the reptile. Classifiers, however, have always agreed that there is something unnatural in the best grouping according to a logical system, because it removes from near association animals which have real affinity with each other. Nor can this be surprising, when we remember that by a class of animals is practically understood a certain horizon or grade of complexity of soft structures. So that if the organization of the bird, for instance, has any relation of affinity with mammal or reptile, the relation must be with some specified order of reptile or mammal, and must be due to their all having diverged in the same direction from the common plan, all being the consequence of a line of variation which has preserved parts of the skeleton unaltered for them all, while the soft parts have become more and more complex, in such ways that the ordinal stem has been divided at intervals into parts which are successively named, it may be, fish, reptile, and bird. If there is foundation for such a view, there can be no such close osteological resemblance between the different natural groups of animals upon the same horizon of organization as there must be between some animals upon that horizon and some animals upon another horizon. This proposition may be exemplified by a diagram of a hand, where there may be supposed to be five stems, springing from a common plan, and it might be better exemplified by taking the entire limb as a type, where the humerus would stand for the common plan. Such a diagram expresses the idea that



the resemblance between the different groups of reptiles, for instance, is a correspondence of homologous parts, and no evidence of the orders having had an immediate parentage in common. Such a doctrine invites investigation. Here I can but state it, and try to show hereafter in what way such portions of it as practically concern the student of reptile bones may be profitably studied.

IV.—*Proposed Name for the Sponge-animal, viz. "Spongozoon;" also on the Origin of Thread-cells in the Spongiadæ.* By H. J. Carter, F.R.S. &c.

As it has now been satisfactorily determined that the Spongiadæ are animals and not plants, and the form of the animal which produces them has also been determined, it becomes necessary to give that form a specific name, and to define the animal, in order that henceforth both may not only be used by the zoologist, but by the comparative anatomist, whose lectures without such additions now cannot be considered complete, the time having passed for the comparative anatomist and the botanist to dispute respecting the kingdom to which this class of beings may belong.

The name that I would propose for this purpose is "spongozoon," which is only the Greek rendering of "sponge-animal," but retaining "sponge" for the root will ever ally it to the Spongiadæ, and thus aid the memory by associations which any other term differently compounded would not do.

Spongozoon, or the sponge-animal, then, I first pointed out in *Spongilla*, in 1857 (Annals, vol. xx. p. 28, pl. 1. fig. 4), wherein it is shown that it is a granuliferous polymorphic body possessing a nucleus and one or more contracting vesicles (p. 30), that it exists in communities of a spherical form with a common circular aperture (figs. 2, 3, 5), in countless numbers, in the sarcode of the sponge (fig. 1), and that it is capable of taking into its body crude material and of discharging the undigested portions after the manner of *Amœba*; lastly, that the circular aperture opens and closes itself as required.

Then, in 1859 (Annals, vol. iii. p. 14, pl. 1. fig. 12), the same monociliated body is described and figured with two ear- or spine-like points of its sarcode, one on each side the cilium, which, I might also add, *now* stands in my journal as it was figured "Aug. 12, 1854," although not published until 1859; and that I had been previously acquainted with the existence of the spines may be seen by the following passage in the paper to which I have last referred, viz.:—"But there